

Spiders in wheat fields and semi-desert in the Negev (Israel)

Therese Pluess^{1,3}, Itai Opatovsky², Efrat Gavish-Regev², Yael Lubin² and Martin H. Schmidt¹: ¹University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland; ²Mitrani Department of Desert Ecology, Ben-Gurion University of the Negev, 84990 Midreshet Ben-Gurion, Israel

Abstract. Intensively cultivated arable land and semi-desert are two dominant habitat types in the arid agroecosystem in the northwest Negev Desert (Israel). The present study compares activity-densities and species richness of spiders in these distinctive habitat types. Sixteen wheat fields and twelve locations in the semi-desert were sampled during the winter growing season of wheat. Semi-desert habitats had more spider species and higher spider activity-densities than irrigated wheat fields. The majority of spider families, namely Gnaphosidae, Thomisidae, Salticidae, Zodariidae, Philodromidae, Dysderidae, and Clubionidae had significantly higher activity-densities in the semi-desert compared to wheat. Only two families, the Linyphiidae that strongly dominated the arable spider community and Corinnidae had higher activity-densities in wheat than in semi-desert. Out of a total of 94 spider species, fourteen had significantly higher activity-densities in semi-desert than in wheat fields and eight species had significantly higher activity-densities in wheat fields than in semi-desert. Spider families and species that dominated the semi-desert communities also occurred in the wheat fields but at lower activity-densities. In conclusion, the semi-desert is a potential source of spider species and families that may immigrate into arable fields during winter. In particular, active hunting spiders may be sustained in crops through immigration from nearby semi-desert habitats.

Keywords: Araneae, biodiversity, desert agroecosystem, habitat preference

Spiders rapidly colonize new habitats, which makes them important natural enemies of pest arthropods in annual crops. Because arable land is an ephemeral habitat, spider populations in crops are frequently depleted (Thomas & Jepson 1997; Marc et al. 1999; Thorbek & Bilde 2004). Owing to their high mobility, spiders are among the first predators to recolonize crop fields after management practices (Öberg & Ekbohm 2006). However, intensification of agriculture in the past decades has led to more uniform landscapes, larger fields of monocultures, loss of natural habitats, and an increase in chemical and physical disturbance of crop habitats. These factors have mostly negative effects on spider densities and species richness in arable land (Topping & Lövei 1997; Marc et al. 1999).

Most arthropods persist more readily in habitats with perennial, structurally rich vegetation and litter layer than in uniform crop fields with a bare soil surface. The availability of non-crop habitats in agricultural landscapes is therefore crucial for arthropods, including spiders (Luczak 1979; Schmidt & Tscharnke 2005a). Non-crop habitats act as refuges where animals can find hiding places from adverse conditions and build up higher population levels. With only a few exceptions, spiders that dominate Central European arable crops depend on perennial habitats for overwintering (Schmidt & Tscharnke 2005a). Woods, hedgerows, field margins, or fallows act as biodiversity reservoirs for animals and plants in agricultural landscapes because they are nearly undisturbed and temporally persistent (Bianchi et al. 2006). Indeed, previous studies showed that spider density and species richness are reduced in arable land compared to neighboring semi-natural habitats with perennial vegetation (Topping & Lövei 1997; Pfiffner & Luka 2000; Lemke &

Poehling 2002; Clough et al. 2005; Schmidt & Tscharnke 2005a; Öberg 2007; Öberg et al. 2007).

Habitat relations of spiders are well studied in agroecosystems of temperate climate zones. In contrast, knowledge of spider communities in arid agroecosystems is still scarce (Gavish-Regev et al. 2008). Differences in habitat conditions between crops and other habitats are more pronounced in arid than in temperate agroecosystems. Here, we present a replicated comparison of spider communities in wheat fields and semi-desert habitats, the two dominant habitat types in the northwest Negev. We tested for differences in species richness and activity-densities of spider families and species. In the Negev Desert, the distribution of spiders across crops and natural habitats may differ from that found in temperate climate for a number of reasons. For example, differences in moisture and primary productivity between cropland and natural habitats are more pronounced in the arid Negev desert compared to most other climatic zones. Arable land in the northwest Negev is intensely managed with high inputs of fertilizers and irrigation. Owing to mild winters, two crops are usually grown within a year, doubling the disturbance events in arable land compared to the one-year crop cycles in temperate climates. The semi-desert on the other hand is characterized by a long dry season during which plant growth comes to a halt. Rains fall from November to March, inducing growth of annual vegetation. Locally adapted arthropods – herbivores and their predators alike – are most active in spring (March–April), following the winter rains (Levy 1985, 1998).

The highly productive wheat fields might attract herbivores that will attract predators, spiders included. However, spider immigration and population growth is counteracted by the high disturbance regime of arable land. Since semi-desert is the native habitat type, the majority of spider families and species should be adapted to it and therefore reach higher activity-densities in semi-desert than in arable land. The following hypotheses were tested:

³Current address: University of Fribourg, Ch. du Musée 10, CH-1700 Fribourg, Switzerland. E-mail: therese.pluess@unifr.ch

1. Spider activity-density is higher in semi-desert than in wheat fields.
2. Species richness is higher in semi-desert than in wheat fields.
3. The majority of families and species prefer semi-desert over wheat fields.

METHODS

Study sites.—Spiders were sampled in sixteen fields of winter wheat (*Triticum aestivum* L.) and at twelve locations in natural semi-arid habitat in the northwestern Negev Desert in Israel. The sampling sites were scattered over an area of 30 × 30 km in a region with intensive agriculture northwest of the city of Beer Sheva (31°14'N, 34°45'E). This area is dominated by large fields of mostly annual crops. Two crops are grown within a year. The summer crops typically consist of cotton (*Gossypium* spp.), sunflowers (*Helianthus annuus*), melons (*Cucumis* spp.) or peanuts (*Arachis hypogaea*). In the winter months, mostly potatoes (*Solanum tuberosum*) and winter wheat are grown. The wheat is sown in November but germination and growth is induced by rain, usually in late November. If it does not rain in due time, farmers irrigate the fields to trigger growth. Depending on the availability of water, some fields are not irrigated or irrigated only occasionally. The wheat is harvested either as green fodder in March or in May–June for the grain. Management of the sampled wheat fields varied but no insecticide spraying was applied during the entire sampling season. All but four wheat fields were irrigated. The soils of the fields consisted of loess with varying proportions of sand. Semi-desert habitat is composed of loess and sandy soils and is mainly found along dry river beds (wadis) or borders on open semi-desert which is used as military training area. Nature reserves are part of the study area in the southwest and the north. Semi-desert habitats are scattered with perennial shrubs and geophytes. In some wadis eucalyptus and acacia trees were planted in recent decades. Annual vegetation consists of grass and herbaceous species and appears after winter rains. At the first sampling in mid-December, the semi-desert was devoid of green vegetation, while wheat growth had been triggered by irrigation and on average, the wheat was 16 cm (± 2.3 SE) high. By the second sampling in the second half of January, rain had induced plant growth in the semi-desert. At the third sampling in the second half of February, vegetation cover was estimated in both habitat types. Vegetation in the semi-desert consisted of 65% (± 5.2 SE) cover of annual vegetation and 1.4% (± 0.5 SE) of perennial vegetation. The wheat in the sampled fields covered 83% (± 7.4 SE) of the surface and was 83 cm (± 5.5 SE) high. Most semi-desert habitats are grazed by Bedouin sheep and goats. The study sites were spatially interspersed to avoid climatic differences between natural and arable sampling sites and to cover the range of climatic conditions in the area (Fig. 1). Landscapes around the study sites varied from crop-dominated to semi-desert dominated. The influence of landscape composition on the spider assemblages will be dealt with elsewhere.

Sampling.—Spiders were sampled by pitfall traps in sixteen wheat fields and twelve sites in the semi-desert. Twenty traps per site were situated at least 50 m from the border of the

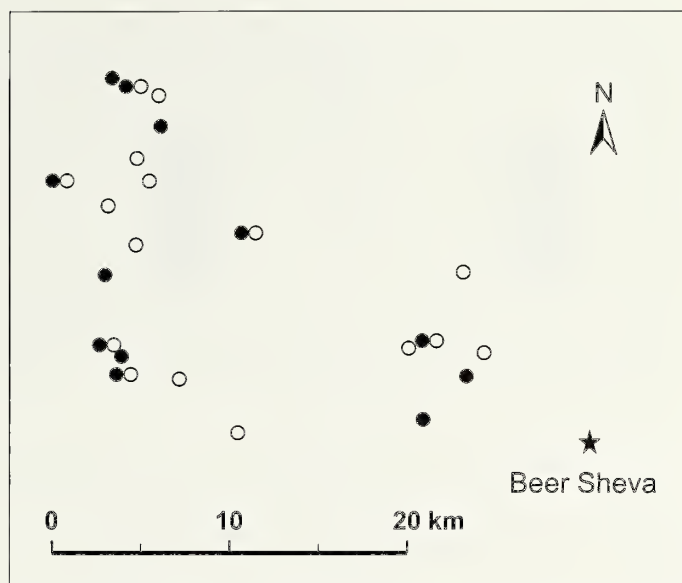


Figure 1.—Distribution of sampling sites in the northwest Negev. Open circles symbolize sampling sites in wheat fields and filled circles symbolize samplings sites in semi-desert.

habitat. They were arranged in four subsets consisting of four traps in a square of 2 m edge length and a fifth trap placed in the centre of the square. Subsets were about 12 m apart. The traps were 10 cm deep with an opening diameter of 9 cm. The traps were buried in the ground such that the rim was level with ground surface and contained 150 ml of 50% ethylene glycol with a drop of detergent as trapping liquid. The traps were opened three times for one week each during the growing season of the winter wheat. The first sampling was done in mid-December, the second in the second half of January and the third in the second half of February. Upon retrieval, spiders were transferred to 70% ethanol. All individuals were identified to family and adult individuals to species or morphospecies (Levy 1985, 1998; Roberts 1995; Dippenaar-Schoeman & Jocque 1997; Proszynski 2003). The nomenclature followed Platnick (2008). Voucher specimens are deposited in the Arachnid Collection at Mitrani Department of Desert Ecology, Ben-Gurion University of the Negev and in the National Collection of Arachnids at the Hebrew University of Jerusalem, Israel.

Analyses.—The captures from the twenty traps and three sampling sessions were summed up for each site. Species richness, overall spider activity-densities and activity-densities per family were compared between the two habitat types using exact significance levels from Mann-Whitney U tests because assumptions for parametric tests were not always met (SPSS Inc. 2005). On the species level, the overall difference in spider communities between wheat fields and semi-desert was assessed with a multivariate redundancy analysis (RDA) and Monte-Carlo permutation test using the program CANOCO (ter Braak & Smilauer 2002). As the overall difference in spider communities between the two habitats was significant, habitat preference of each species could be tested with exact Mann-Whitney U tests using species-wise error rates (Moran 2003). Standard errors are given in text, tables and figures.

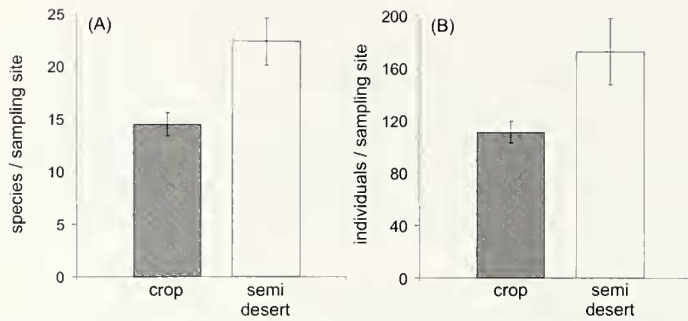


Figure 2.—(A) Species richness and (B) spider activity-density per sampling site in wheat fields versus semi-desert.

RESULTS

In total, 4093 spiders belonging to 26 families and 94 species were caught. Species richness was 54% higher in the semi-desert than in the wheat fields (exact Mann-Whitney U tests; $Z_{1,27} = -2.4$, $P = 0.013$; Fig. 2A). Spider activity-density showed a very similar pattern, and was 55% higher in the semi-desert than in wheat fields ($Z_{1,27} = -1.9$, $P = 0.058$, Fig. 2B). Of the thirteen most common families, only Linyphiidae ($Z_{1,27} = -3.3$, $P < 0.001$; Fig. 3) and Corinnidae ($Z_{1,27} = -2.0$, $P = 0.04$) showed significantly higher numbers in wheat fields. In contrast, eight families reached significantly higher activity-densities in the semi-desert than in crops. In the order of their overall activity-density, these were ground spiders (Gnaphosidae) $Z_{1,27} = -3.3$, $P = 0.001$, crab spiders (Thomisidae) $Z_{1,27} = -3.7$, $P < 0.001$, jumping spiders

(Salticidae) $Z_{1,27} = -2.2$, $P = 0.024$, ant spiders (Zodariidae) $Z_{1,27} = -4.4$, $P < 0.001$, running crab spiders (Philodromidae) $Z_{1,27} = -3.2$, $P = 0.001$, woodlouse spiders (Dysderidae) $Z_{1,27} = -3.9$, $P < 0.001$, running foliage spiders (Liocranidae) $Z_{1,27} = -2.4$, $P = 0.01$ and sac spiders (Clubionidae) $Z_{1,27} = -3.5$, $P < 0.001$. Wolf spiders (Lycosidae), cobweb spiders (Theridiidae), and giant crab spiders (Sparassidae) showed no significant habitat preference. On the species level, spider communities differed significantly between wheat fields and semi-desert (RDA; $F_{1,27} = 7.5$, $p = 0.0001$). The difference accounted for 22.4% of all variation in community composition. Out of the 94 species found, eight species had significantly higher activity-densities in wheat fields than in semi-desert (Table 1). Six of them were sheetweb spiders, including the overall most common *Aliorauus pastoralis* and the exotic North American species *Mermessus denticulatus*. Fourteen species from six families had significantly higher activity-densities in semi-desert than in wheat fields (Table 1).

DISCUSSION

In the northwest Negev, spider activity-density and species richness were higher in the semi-desert than in winter wheat. Ground spiders (Gnaphosidae), a species rich family in Israel, contributed most to the overall activity-density in the semi-desert. In addition, crab spiders (Thomisidae) and ant spiders (Zodariidae) reached high activity-densities in the semi-desert. Despite the preference of most families for the semi-desert, they also occurred in wheat fields at low activity-densities (Fig. 3). Probably, immigration from semi-desert into wheat fields is

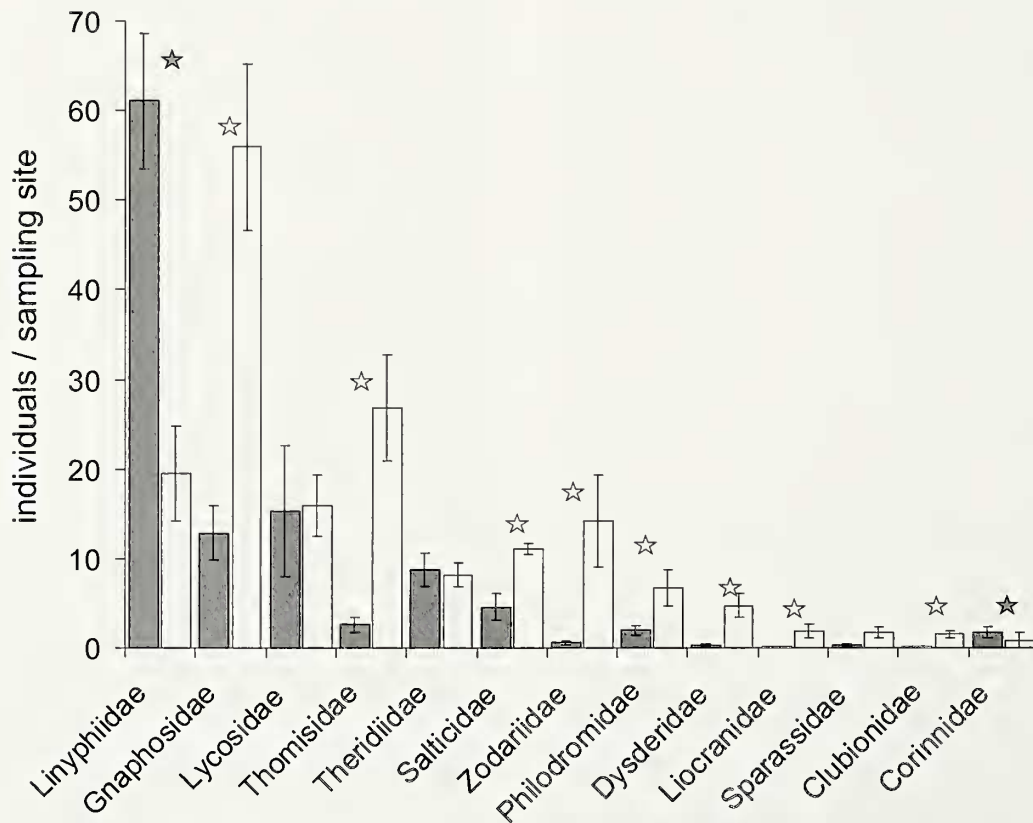


Figure 3.—Activity-densities per sampling site of spider families in wheat fields (grey) versus semi-desert (white). Filled stars represent a significant preference for the crop; open stars represent significant preference for semi-desert.

Table 1.—Average activity-densities (\pm SE) of spider species in the $n = 16$ wheat fields and $n = 12$ semi-desert locations, corresponding to 420 trap-days per location. Activity-densities that are significantly higher in one of the habitat types are given in bold. Z and P are according to exact Mann-Whitney U tests. Species with less than ten individuals (number of individuals in wheat fields versus semi-desert in parentheses): Agelenidae: *Lycosoides coarctata* (Dufour 1831) (1,0), Araneidae: *Hypsosinga albovittata* (Westring 1851) (0,1), Clubionidae: *Clubiona genevensis* L. Koch 1866 (0,5), Dictynidae: *Lathys* sp11 (0,2), Dysderidae: *Dysdera* sp12 (1,5), *Tedia abdominalis* Deeleman-Reinhold 1988 (1,8), *Tedia oxygnatha* Simon 1882 (2,2), Filistatidae: sp13 (0,1), Gnaphosidae: *Anagraphis palleus* Simon 1893(1,0), *Drassodes lutescens* (C.L. Koch 1839) (1,3), *Haplodrassus dalmatensis* (L. Koch 1866) (5,4), *Odontodrassus mundulus* (O. Pickard-Cambridge 1872) (0,7), *Pterotricha conspersa* (O. Pickard-Cambridge 1872) (0,1), *Talanites* sp14 (0,2), *Trachyzelotes cf javartensis* (Kroneberg 1875) (0,1), Linyphiidae: *Diplocephalus cf protuberans* (O. Pickard-Cambridge 1875) (4,0), *Leptyphantes* sp15 (3,1), *Leptyphantes* sp16 (5,4), *Pelecopsis* sp17 (1,0), *Sintula* sp18 (3,1), *Thaunatoncus* sp19. (0,3), *Thammatancus* sp20 (1,1), sp21 (1,6), sp22 (0,1), sp23 (1,0), Liocranidae: *Mesiotelus* sp24 (0,5), Lyeosidae: sp25 (1,0), *Trochosa* sp26 (2,1), Nemesiidae: *Nemesia* sp27 (0,1), Philodromidae: *Thanatus meronensis* Levy 1977 (0,1), sp28 (1,0), Prodidomidae: sp29 (1,0), Salticidae: *Achrillus conveniens* (O. Pickard-Cambridge 1872) (0,1), *Achrillus politiventris* (O. Pickard-Cambridge 1872) (0,1), *Pellenes simoni* L. Koch 1882 (1,7), *Salticus olivaceus* (L. Koch 1867) (0,1), *Salticus propinquus* Lucas 1846 (0,6), Sicariidae: *Loxosceles* sp30 (0,1), Theridiidae: *Enoplognatha deserta* Levy & Amitai 1981 (1,1), *Euryopis episinoides* (Walckenaer 1847) (0,1), *Latrodectus tredecimguttatus* (Rossi 1790) (0,1), *Steatoda erigoniformis* (O. Pickard-Cambridge 1872) (1,0), *Steatoda latifasciata* (Simon 1873) (4,0), *Steatoda naura* (Simon 1909) (1,0), *Steatoda triangulosa* (Walckenaer 1802) (1,0), *Theridion nigropunctatum* Lucas 1846 (0,1), Thomisidae: *Ozyptila judaea* Levy 1975 (0,4), *Ozyptila omega* Levy 1975 (0,2), *Xysticus caperatus* Simon 1875 (1,0), *Xysticus edax* (O. Pickard-Cambridge 1872) (1,7), *Xysticus keupeleni* Thorell 1872 (0,1), *Xysticus promiscuus* O. Pickard-Cambridge 1876 (0,1), Zodariidae: *Zodarium litipes* (O. Pickard-Cambridge 1872) (0,1), Zoropsidae: *Zoropsis lutea* (Thorell 1875) (0,2).

Family	Species	Wheat fields	Semi-desert	Z	P
Corinnidae	<i>Phrurolithus</i> sp1	1.75 \pm 0.65	0.00 \pm 0.00	-2.8	0.007
	Corinninae sp2	0.00 \pm 0.00	0.83 \pm 0.83	-1.2	0.429
Dictynidae	sp3	0.00 \pm 0.00	0.83 \pm 0.75	-1.7	0.175
Dysderidae	<i>Dysdera westringi</i> O. Pickard-Cambridge 1872	0.13 \pm 0.09	1.58 \pm 0.29	-3.9	0.000
	<i>Harpactea</i> sp4	0.00 \pm 0.00	1.83 \pm 0.91	-2.4	0.024
Gnaphosidae	<i>Haplodrassus mediterraneus</i> Levy 2004	0.56 \pm 0.22	1.50 \pm 0.61	-1.3	0.219
	<i>Haplodrassus morosus</i> (O. Pickard-Cambridge 1872)	0.31 \pm 0.18	1.67 \pm 0.80	-1.2	0.204
	<i>Micaria corvina</i> Simon 1878	0.25 \pm 0.19	14.42 \pm 5.60	-3.2	0.001
	<i>Micaria ignea</i> (O. Pickard-Cambridge 1872)	0.06 \pm 0.06	0.92 \pm 0.50	-1.9	0.101
Linyphiidae	<i>Micaria pallipes</i> (Lucas 1846)	0.00 \pm 0.00	1.58 \pm 0.73	-2.8	0.008
	<i>Miosia spinosissima</i> (Simon 1878)	1.06 \pm 0.87	3.83 \pm 0.90	-3.1	0.001
	<i>Alioranus pastoralis</i> (O. Pickard-Cambridge 1872)	21.50 \pm 3.37	7.17 \pm 2.04	-3.0	0.002
	<i>Bathypantes cf extricates</i> (O. Pickard-Cambridge 1876)	0.75 \pm 0.28	0.00 \pm 0.00	-2.6	0.017
	<i>Erigone dentipalpis</i> (Wider 1834)	0.69 \pm 0.22	0.00 \pm 0.00	-2.6	0.016
	<i>Gongylidiellum</i> sp5	16.56 \pm 5.12	0.08 \pm 0.08	-3.3	0.001
	<i>Mecopisthes monticola</i> Bosmans 1993	1.56 \pm 1.38	5.67 \pm 3.72	-0.9	0.463
	<i>Meioneta pseudonrestris</i> (Wunderlich 1980)	0.75 \pm 0.27	0.75 \pm 0.28	-0.2	0.901
	<i>Mermessus denticulatus</i> (Banks 1898)	6.81 \pm 2.48	0.08 \pm 0.08	-3.2	0.001
	<i>Pelecopsis cf inedita</i> (O. Pickard-Cambridge 1875)	0.44 \pm 0.32	0.75 \pm 0.75	-0.6	0.613
Liocranidae	<i>Pelecopsis</i> sp6	0.69 \pm 0.24	0.67 \pm 0.43	-0.8	0.467
	<i>Trichoncoides piscator</i> (Simon 1884)	8.13 \pm 2.07	0.08 \pm 0.08	-3.5	0.000
	sp7	0.25 \pm 0.17	2.67 \pm 1.05	-2.3	0.013
Lycosidae	<i>Liocranum</i> sp8	0.06 \pm 0.06	0.92 \pm 0.45	-1.9	0.085
	<i>Alopecosa cf albofasciata</i> (Brullé 1832)	0.06 \pm 0.06	1.00 \pm 0.44	-2.3	0.041
Philodromidae	<i>Pardosa cf proxima</i> (C.L. Koch 1847)	9.50 \pm 5.88	0.17 \pm 0.17	-2.9	0.004
	sp9	1.00 \pm 0.52	6.67 \pm 2.04	-3.4	0.000
	<i>Thanatus vulgaris</i> Simon 1870	0.06 \pm 0.06	1.00 \pm 0.59	-1.9	0.085
Salticidae	<i>Achrillus cf aeruginosus</i> (Simon 1871)	3.56 \pm 1.18	5.58 \pm 1.76	-0.9	0.394
Sparassidae	<i>Micrommuata formosa</i> Pavesi 1878	0.19 \pm 0.10	1.42 \pm 0.60	-1.9	0.057
Theridiidae	<i>Enoplognatha gemina</i> Bosmans & Van Keer 1999	3.50 \pm 0.92	3.50 \pm 1.06	-0.19	0.863
	<i>Enoplognatha macrochelis</i> Levy & Amitai 1981	1.38 \pm 0.50	0.75 \pm 0.25	-0.2	0.887
	<i>Steatoda albomaculata</i> (De Geer 1778)	1.31 \pm 0.99	0.00 \pm 0.00	-2.1	0.053
	<i>Steatoda paykulliana</i> (Walckenaer 1805)	0.25 \pm 0.11	0.67 \pm 0.43	-0.2	0.710
Thomisidae	<i>Ozyptila patellibidens</i> Levy 1999	0.44 \pm 0.18	5.58 \pm 1.60	-2.9	0.003
	<i>Ozyptila</i> sp10	1.31 \pm 0.69	12.92 \pm 6.37	-0.8	0.452
	<i>Ozyptila tricoloripes</i> Strand 1913	0.25 \pm 0.17	0.75 \pm 0.25	-1.9	0.061
	<i>Xysticus bliteus</i> (Simon 1875)	0.31 \pm 0.18	2.17 \pm 0.91	-2.4	0.019

Table 1.—Continued.

Family	Species	Wheat fields	Semi-desert	Z	P
Zodariidae	<i>Xysticus cristatus</i> (Clerck 1757)	0.00 ± 0.00	1.83 ± 0.95	-2.8	0.008
	<i>Xysticus xerodermus</i> Strand 1913	0.00 ± 0.00	1.75 ± 0.65	-3.4	0.001
	<i>Lachesana rufiventris</i> (Simon 1873)	0.13 ± 0.13	0.75 ± 0.45	-1.4	0.242
	<i>Ranops exers</i> (O. Pickard-Cambridge 1876)	0.00 ± 0.00	5.83 ± 2.64	-2.8	0.008
	<i>Zodariou uitidhuu</i> (Audouin 1826)	0.00 ± 0.00	2.42 ± 1.57	-2.8	0.008

responsible for the presence of these desert-preferring spiders. Semi-desert, therefore, serves as a source for spider migration into the arable fields and thus contributes to a more diverse spider fauna in wheat fields in this desert agroecosystem (Gavish-Regev 2008). Despite the presence of some desert spiders, the wheat fields were dominated by one family. More than half of the individuals in wheat fields belonged to the sheetweb spiders (Linyphiidae), which showed a strong preference for this habitat. While sheetweb spiders dominate arable land both in Israel and in the temperate zone, the patterns in natural habitats are different. European natural habitats harbor more sheetweb spiders than arable land and act as sources for immigration of these spiders into fields (Schmidt & Tschamtk 2005a). This is not the case in the Negev where it is more likely that wheat fields act as a source for sheetweb spiders to spill over into the semi-desert (Tschamtk et al. 2005; Rand & Louda 2006; Rand et al. 2006).

The disturbance regime in arable land in the northern Negev is even higher than in Europe because two crops are grown per year. This means that operations such as harvest and tillage occur twice instead of once per year. Only very few families may be able to cope with this degree of disturbance. Sheetweb spiders show traits of typical pioneers and just as in temperate climate zones (Samu & Szinetar 2002; Nyffeler & Sunderland 2003; Schmidt & Tschamtk 2005a), they were also dominant in disturbed arable land sampled in the present study. However, the mechanism responsible for this dominance in the Negev fields may be different from temperate climate zones. Gavish-Regev et al. (2008) found similar numbers of sheetweb spiders in open traps and in closed emergence traps that were installed after crop sowing, which suggests that sheetweb spiders do not immigrate, but are residents in crop fields in the Negev Desert. Just like other arthropods, sheetweb spiders are negatively affected by mechanical management practices in the crops, but they apparently rebuild populations from egg sacs or individuals that survived sowing. This is a different mechanism than in temperate climate zones, where immigration by ballooning appears to result in the high dominance of sheetweb spiders in arable land (Nyffeler & Sunderland 2003; Schmidt & Tschamtk 2005b).

Spiders are sensitive to habitat structure (Marc et al. 1999; Bell et al. 2001). During the crop season, the ground of wheat fields is bare with hardly any litter. While sheetweb spiders can cope with the lack of litter, other ground dwellers avoid such habitats. Together with the high disturbance regime this can explain the low activity-densities in ground spiders (Gnaphosidae), crab spiders (Thomisidae) and sac spiders (Clubionidae) in wheat fields. Vegetation structure and litter layer determine microclimatic conditions that are important for spiders (Bell et al. 2001). Low humidity is one

of the main factors limiting spider survival (Almquist 1971; Cardoso et al. 2007). Spiders avoid desiccation by seeking taller vegetation where humidity is higher (De Keer et al. 1989). The risk of desiccation is accentuated in arid environments and probably even more so for small species such as sheetweb spiders, which preferred the more humid and densely vegetated wheat fields over semi-desert. Except for the exotic *M. denticulatus*, little is known about the origin of sheetweb spider species in the agricultural land of the Negev. Sheetweb spiders are mostly a sub-arctic group, adapted to moderate temperatures and high humidity (Nyffeler & Sunderland 2003). Sheetweb spiders that occurred in the Negev before the development of agriculture were probably concentrated to a few relatively humid habitats. This pre-adaptation may now allow them to dominate arable land in the Negev desert. As an exception, one species of sheetweb spiders (morphospecies sp7) preferred semi-desert over wheat fields. In contrast to the majority of sheetweb spiders, active hunting spiders predominate in warmer regions because their foraging strategy is more efficient at warmer temperatures (Nyffeler & Sunderland 2003). Shady, slightly cooler habitat conditions might therefore have contributed to the low numbers of active hunting spiders in wheat fields.

Spider density is often determined by prey availability (Harwood et al. 2001). The intensive cultivation methods with irrigation and use of fertilizers lead to a high primary production in the studied wheat fields. This potentially attracts herbivores, which could in turn lead to higher prey abundance for spiders. Crop fields in the semi-desert might also, therefore, be an attractive habitat for desert spiders. Although spiders are generalist predators, some families have evolved prey preferences. The dominant Salticidae species in the present study is *Aelurillus aeruginosus* (Simon 1871), a predator of ants (Hymenoptera: Formicidae) (Li et al. 1999). *Aelurillus aeruginosus* reached higher activity-densities in the natural habitat. This corresponds to the habitat preference of their prey, because ants are usually scarce on ploughed soil (Dauber et al. 2005). Low activity-densities of ants in crop fields are likely to also explain the preference of ant spiders (Zodariidae) for the natural habitat, because this family also feeds predominately on ants. Small spiders in general and sheetweb spiders in particular feed mainly on soft bodied, small sized springtails (Collembola) (Sanders & Platner 2007). These arthropods are rare on dry soils and thus food for sheetweb spiders is scarce in semi-deserts (Nyffeler & Sunderland 2003). Finally, the semi-desert is the prevailing habitat type of the arid climate zone to which Negev spiders are adapted. One means of adaptation may be strongly seasonal activity patterns (Jiménez & Lobo 2006; Langlands et al. 2006; Cardoso et al. 2007).

In conclusion, spider diversity is concentrated in natural habitats not only in temperate climates but also in the semi-desert agroecosystem of the Negev. With respect to spider activity-density, a strong preference of sheetweb spiders for arable fields contrasted with the preference of the remaining spider families for the semi-desert. Accordingly, especially wandering spiders in desert crops are expected to benefit from the conservation of semi-desert in the agricultural landscape.

ACKNOWLEDGMENTS

We would like to thank all farmers who allowed us to access their fields. Special thanks goes to Iris Museli, Gershom Levy and Milan Rezac for assistance in spider identification. We thank two anonymous referees who provided constructive comments on an earlier version of the manuscript. This study was supported by the Berne University Research Foundation and the Mitrani Department for Desert Ecology. This is publication no. 617 of the Mitrani Department of Desert Ecology.

LITERATURE CITED

- Almquist, S. 1971. Resistance to desiccation in some dune-living spiders. *Oikos* 22:225–229.
- Bell, J.R., C.P. Wheeler & W.R. Cullen. 2001. The implications of grassland and heathland management for the conservation of spider communities: a review. *Journal of Zoology* 255:377–387.
- Bianchi, F.J.J.A., C.J.H. Booji & T. Tscharrntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B* 273:1715–1727.
- Cardoso, P., I. Silva, N.G. de Oliveira & A.R.M. Serrano. 2007. Seasonality of spiders (Araneae) in Mediterranean ecosystems and its implications in the optimum sampling period. *Ecological Entomology* 32:516–526.
- Clough, Y., A. Kruess, D. Kleijn & T. Tscharrntke. 2005. Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. *Journal of Biogeography* 32:2007–2014.
- De Keer, R., M. Alderweireldt, K. Decler, H. Segers, K. Desender & J.P. Maelfait. 1989. Horizontal distribution of the spider fauna of intensively grazed pastures under the influence of diurnal activity and grass height. *Journal of Applied Entomology* 107:455–473.
- Dippenaar-Schoeman, A.S. & R. Jocqué. 1997. African Spiders. An Identification Manual. ARC – Plant Protection Research Institute Handbook Number 9. Johannesburg. 392 pp.
- Gavish-Regev, E., Y. Lubin & M. Coll. 2008. Migration patterns and functional groups of spiders in a desert agroecosystem. *Ecological Entomology* 33:202–212.
- Harwood, J.D., K.D. Sunderland & W.O. C Symondson. 2001. Living where the food is: web-location by linyphiid spiders in relation to prey availability in winter wheat. *Journal of Applied Ecology* 38:88–99.
- Jiménez-Valverde, A. & J.M. Lobo. 2006. Establishing reliable spider (Araneae, Araneidae and Thomisidae) assemblage sampling protocols: estimation of species richness, seasonal coverage and contribution of juvenile data to species richness and composition. *Acta Oecologica* 30:21–32.
- Langlands, P.R., K.E.C. Brennan & D.J. Person. 2006. Spiders, spinifex, rainfall and fire: long-term changes in an arid spider assemblage. *Journal of Arid Environments* 67:36–59.
- Lemke, A. & H.-M. Poehling. 2002. Sown weed strips in cereal fields: overwintering site and “source” habitat for *Oedothorax apicatus* (Blackwall) and *Erigone ara* (Blackwall) (Araneae: Erigonidae). *Agriculture, Ecosystems and Environment* 90:67–80.
- Levy, G. 1985. Araneae: Thomisidae. Israel Academy of Sciences and Humanities, Jerusalem. 114 pp.
- Levy, G. 1998. Araneae: Theridiidae. Israel Academy of Sciences and Humanities, Jerusalem. 226 pp.
- Li, D., R.R. Jackson & D.P. Harland. 1999. Prey-capture techniques and prey preferences of *Aelurillus aerugiuousus*, *A. cognatus* and *A. kochii*, ant-eating jumping spiders (Araneae: Salticidae) from Israel. *Israel Journal of Zoology* 34:341–359.
- Marc, P., A. Canard & F. Ysnel. 1999. Spiders (Araneae) useful for pest limitation and bioindication. *Agriculture, Ecosystems & Environment* 74:229–273.
- Moran, M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403–405.
- Nyffeler, M. & K.D. Sunderland. 2003. Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. *Agriculture, Ecosystems & Environment* 95:579–612.
- Öberg, S. 2007. Diversity of spiders after spring sowing - influence of farming system and habitat type. *Journal of Applied Entomology* 131:524–531.
- Öberg, S. & B. Ekbom. 2006. Recolonization and distribution of spiders and carabids in cereal fields after spring sowing. *Annals of Applied Biology* 149:203–211.
- Öberg, S., B. Ekbom & R. Bommarco. 2007. Influence of habitat type and surrounding landscape on spider diversity in Swedish agroecosystems. *Agriculture, Ecosystems & Environment* 122:211–219.
- Pfiffner, L. & H. Luka. 2000. Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agriculture, Ecosystems & Environment* 78:215–222.
- Platnick, N.I. 2008. The World Spider Catalog, Version 8.5. American Museum of Natural History, New York. Online at <http://research.amnh.org/entomology/spiders/catalog/INTRO1.html>.
- Proszynski, J. 2003. Salticidae (Araneae) of the Levant. *Annales Zoologici (Warszawa)* 53:1–180.
- Rand, T.A. & S.M. Louda. 2006. Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. *Conservation Biology* 20:1720–1729.
- Rand, T.A., J.M. Tylianakis & T. Tscharrntke. 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology Letters* 9:603–614.
- Roberts, M.J. 1995. Spiders of Britain and Northern Europe. Harper Collins, London. 383 pp.
- Samu, F. & C. Szinetar. 2002. On the nature of agrobiont spiders. *Journal of Arachnology* 30:389–402.
- Sanders, D. & C. Platner. 2007. Intraguild interactions between spiders and ants and top-down control in a grassland food web. *Oecologia* 150:611–624.
- Schmidt, M.H. & T. Tscharrntke. 2005a. The role of perennial habitats for Central European farmland spiders. *Agriculture, Ecosystems and Environment* 105:235–242.
- Schmidt, M.H. & T. Tscharrntke. 2005b. Landscape context of sheetweb spider (Araneae: Linyphiidae) abundance in cereal fields. *Journal of Biogeography* 32:467–473.
- ter Braak, C.J.F. & P. Smilauer. 2002. CANOCO Reference Manual: Software for Canonical Community Ordination, Version 4.5. Microcomputer Powers, Ithaca, New York. 500 pp.
- Thomas, C.F.G. & P.C. Jepson. 1997. Field-scale effects of farming practices on linyphiid spider populations in grass and cereals. *Entomologia Experimentalis et Applicata* 84:59–69.
- Thorbeck, P. & T. Bilde. 2004. Reduced numbers of generalist arthropod predators after crop management. *Journal of Applied Ecology* 41:526–538.
- Topping, C.J. & G.L. Lövei. 1997. Spider density and diversity in relation to disturbance in agroecosystems in New Zealand, with a comparison to England. *New Zealand Journal of Ecology* 2:121–128.
- Tscharrntke, T., T.A. Rand & F.J.J.A. Bianchi. 2005. The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. *Annales Zoologici Fennici* 42:421–432.